

Charopid Snails of Mounts Mahermana, Ilapiry, and Vasiha, Southeastern Madagascar, with Description of a New Genus and with Conservation Statuses of Nine Species

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Abstract. Quantitative, replicated altitudinal transects yielded nine charopids, all belonging to the endemic genus *Reticulapex* gen. nov., which is characterized by cross-hatched embryonic sculpture; an extremely elongate fertilization pouch-seminal receptacle complex; nearly basal entry of the vas deferens into, and nearly apical origin of the penial-retractor muscle from, the epiphallus; and deposition of a spiral spermatophore on the mate's penis.

Reticulapex gen. nov. represents the fifth known independent evolution of external sperm exchange within the Stylommatophora. At least some other charopids have internal sperm exchange.

Descriptions are given of *Reticulapex* gen. nov. *apexfortis* sp. nov., *R. compactus* sp. nov., *R. fischerpiettei* sp. nov., *R. flammulatus* sp. nov., *R. lucidus* sp. nov., *R. scaber* sp. nov., *R. subangulatus* sp. nov., *R. ulrichi* (Fischer-Piette, Blanc, Blanc & Salvat, 1994) comb. nov., and *R. villosus* sp. nov.

Description of *Reticulapex* gen. nov. includes the additional new combinations *R. choutardi* (Fischer-Piette, Blanc, Blanc & Salvat, 1994) comb. nov., *R. druggi* (Fischer-Piette, Blanc, Blanc & Salvat, 1994) comb. nov., *R. harananae* (Emberton, 1994) comb. nov., *R. intridi* (Fischer-Piette, Blanc, Blanc & Salvat, 1994) comb. nov., *R. talatai* (Emberton, 1994) comb. nov., *R. vatuvavyae* (Emberton, 1994) comb. nov., and *R. vineti* (Fischer-Piette, Blanc, Blanc & Salvat, 1994) comb. nov.

Distributional data allowed evaluation of each of the nine Mahermana-Ilapiry-Vasiha charopid species for its conservation status, applying the latest IUCN criteria. Two species are proposed as Critically Endangered and seven as Endangered.

INTRODUCTION

This paper is the third in a series of four that identify and describe the species reported on as morphospecies by Emberton et al. (1996, 1999) and Emberton (1997). This paper treats the Mahermana-Ilapiry-Vasiha charopids and evaluates each charopid species for conservation status.

MATERIALS AND METHODS

Collecting methods have been detailed by Emberton et al. (1996). Sixteen stations were collected and numbered in the "Tol" series (for Tolagnaro = Fort Dauphin, the nearest city). These stations have been mapped by Emberton et al. (1996) and by Emberton (1997). To shorten the taxonomic descriptions, stations are described briefly below. Catalogued station numbers, given in parentheses, are in the series of the Molluscan Biodiversity Institute

(MBI). All stations were restricted to primary forest that had no more than limited selective cutting. Ecological data are given by Emberton (1997:table 1). All stations are in Madagascar: Tuléar Province. Mount Mahermana (Vohimena Chain) is northeast of the village of Esetra, Ilapiry (Vohimena Chain) is west of Mahialambo, and Vasiha (Anosy Chain) is west of Malio. Latitude and longitude are given in degrees, minutes, and seconds.

Tol-1 (= MBI 373). Summit of Mt. Mahermana, 340 m, 24°26'12"S, 47°13'13"E.

Tol-1-2 (= MBI 390). Incidental collecting between Tol-1 and Tol-2.

Tol-2 (= MBI 374). Slope of Mt. Mahermana, 300 m, 24°26'17"S, 47°13'10"E.

Tol-3 (= MBI 375). Slope of Mt. Mahermana, 200 m, 24°26'15"S, 47°13'04"E.

Tol-3-4 (= MBI 389). Incidental collecting between Tol-3 and Tol-4.

Tol-4 (= MBI 376). Valley on Mt. Mahermana, 100 m, 24°26'22"S, 47°12'41"E.

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Tol-5 (= MBI 377). Summit of Mt. Ilapiry, 540 m, 24°51'40"S, 47°00'20"E.

Tol-sub-5 (= MBI 391). Incidental collecting below summit of Mt. Ilapiry, Tol-5.

Tol-6 (= MBI 378). Ridge on Mt. Ilapiry, 500 m, 24°51'33"S, 47°00'27"E.

Tol-7 (= MBI 379). Ridge, valley, and slope on Mt. Ilapiry, 400 m, 24°51'27"S, 47°00'38"E.

Tol-8 (= MBI 380). Slope of Mt. Ilapiry, 300 m, 24°51'36"S, 47°00'40"E.

Tol-7-9 (= MBI 392). Incidental collecting between Tol-7 and Tol-9.

Tol-9 (= MBI 381). Slope of Mt. Ilapiry, 200 m, 24°51'39"S, 47°00'46"E.

Tol-10 (= MBI 382). Lower summit of Mt. Vasiha, 860 m, 24°55'18"S, 46°44'19"E.

Tol-11 (= MBI 383). Slope of Mt. Vasiha, 700 m, 24°55'23"S, 46°44'27"E.

Tol-12 (= MBI 384). Slope of Mt. Vasiha, 500 m, 24°55'19"S, 46°44'45"E.

Tol-13 (= MBI 385). Valley on Mt. Vasiha, 400 m, 24°55'25"S, 46°44'45"E.

Tol-14 (= MBI 386). Slope of Mt. Vasiha, 300 m, 24°55'37"S, 46°44'49"E.

Tol-15 (= MBI 387). Slope of Mt. Vasiha, 200 m, 24°56'13"S, 46°45'13"E.

Tol-16 (= MBI 388). Slope of Mt. Vasiha, 100 m, 24°56'20"S, 46°46'07"E.

Species identifications and comparisons were made using Fischer-Piette et al. (1994) and Emberton (1994a). For each species, the holotype or a representative shell was photographed in apertural, basal, and side views at either 6.4×, 10×, 16×, or 25× magnification, and in apical view at 40× magnification. Additional specimens were photographed as needed to illustrate shell variation or sculptural features.

Twenty-four shell characters (Table 1; Emberton & Pearce, 1999:fig. 1, 2000:fig. 1) were measured, or measured and calculated, or scored from the photographs or from the shells themselves.

An adult anatomy was available for each of five species. From each, the reproductive system was removed and photographed as it was turned and progressively dissected to expose characters. Thirteen reproductive-anatomical characters (Table 1, Figure 12) were taken from the photographs or from the dissections themselves.

Character matrices were prepared and used to code character-state data into the DELTA system (Dallwitz et al., 1993), which was then used to generate natural-language species descriptions.

For each charopid species, conservation status was evaluated using the new categories and criteria of the International Union for the Conservation of Nature (IUCN, 1996). Ranges were estimated from 1992–1995 distributional data (Emberton, unpublished). Rainforest extent and decline were assessed using Green & Sussman

Table 1

Shell and reproductive characters used in descriptions. Many are illustrated by Emberton & Pearce (1999a:figure 1, 1999b:figure 1).

SHELL

1. Diameter (0.1 mm)
2. Height (0.1 mm)
3. Height/Diameter (0.1)
4. Spire angle (degrees)
5. Whorl periphery shape (round, angular, keeled)
6. Whorl shoulder shape (round, flat)
7. Aperture width parallel to parietal callus (% diameter)
8. Aperture height (perpendicular to parietal callus)/width (0.01)
9. Umbilicus size (% diameter)
10. Whorl number (0.1)
11. Coiling tightness (whorl number/ln diameter)
12. Embryonic whorl number (0.1)
13. Embryonic shell diameter (0.1 mm)
14. First whorl diameter (0.1 mm)
15. Embryonic sculpture
16. Post-embryonic cross-hatch sculpture (absent, faint, moderate, strong)
17. Transverse rib density (number in first 0.1 of body whorl)
18. Rib height (% shell diameter)
19. Rib periostracum locally extended into hair (no, length [% shell diameter])
20. Periostracal hairs unassociated with ribs (number between sutures)
21. Height of periostracal hairs unassociated with ribs (% shell diameter)
22. Conspicuous spiral grooves below periphery of body whorl (no, number)
23. Shell ground color
24. White blotches of color on shell

REPRODUCTIVE SYSTEM

25. Penis length (0.1 mm)
26. Penis length/shell diameter (0.1)
27. Penis width (range, 0.1 mm)
28. Penial sculpture
29. Epiphallus shape and orientation
30. Spermatophore size, shape, and deposition site
31. Penial retractor muscle attachment position
32. Vas deferens entry position and width
33. Atrium length
34. Vagina length
35. Spermathecal duct width and length
36. Spermatheca shape and position
37. Fertilization pouch-seminal receptacle complex shape and length

(1990), Sussman et al. (1994), and the most recently available topographic maps.

SYSTEMATICS

Higher classification follows Ponder & Lindberg (1997) and Nordsieck (1996). Type materials are placed in the United States National Museum, Washington, D.C.

(USNM); temporarily in the Molluscan Biodiversity Institute (MBI), all of whose collections will revert in the near future to the Florida Museum of Natural History, Gainesville; and in the Australian Museum, Sydney (AMS); the Muséum national d'Histoire naturelle, Paris (MNHN); and the Academy of Natural Sciences of Philadelphia (ANSP). For paratype localities, use the MBI catalog number to refer to the station numbers (in parentheses) above. MBI catalog numbers consist of station number, period, species number, D (dry) or A (alcohol-preserved), and when appropriate H (holotype) or P (paratype) or R (representative).

Subclass PULMONATA: Order

STYLOMMATOPHORA

Suborder SIGMURETHRA

Infraorder ACHATINIDA

Superfamily PUNCTOIDEA

Family CHAROPIDAE

Reticulapex Emberton & Pearce, gen. nov.

Trachycystis Pilsbry, 1893 (in part), Fischer-Piette et al., 1994:175–177, 178–184, figs. 71, 73–76.

Pilula Martens, 1898, Emberton, 1994a:168–171, figs. 73–83 (not Fischer-Piette et al., 1994:193–194, figs. 85, 86).
Charopidae n. gen., Emberton, 1996:730, 731, 734, 736.

Type species: *R. villosus* sp. nov.

Other species: *R. apexfortis* sp. nov., *R. choutardi* (Fischer-Piette, Blanc, Blanc & Salvat, 1994) comb. nov., *R. compactus* sp. nov., *R. druggi* (Fischer-Piette, Blanc, Blanc & Salvat, 1994) comb. nov., *R. fischerpiettei* sp. nov., *R. flammulatus* sp. nov., *R. harananae* (Emberton, 1994a) comb. nov., *R. intridi* (Fischer-Piette, Blanc, Blanc & Salvat, 1994) comb. nov., *R. lucidus* sp. nov., *R. scaber* sp. nov., *R. subangulatus* sp. nov., *R. talatai* (Emberton, 1994a) comb. nov., *R. ulrichi* (Fischer-Piette, Blanc, Blanc & Salvat, 1994) comb. nov., *R. vatuvavyae* (Emberton, 1994a) comb. nov., and *R. vineti* (Fischer-Piette, Blanc, Blanc & Salvat, 1994) comb. nov.

Description: Shell diameter ca. 3–18 mm; height/diameter 0.6–0.8. Spire angle 100–150 degrees. Whorl periphery round to slightly angular. Whorl shoulder round to very flat. Aperture width (inside dimension, parallel to a line between the columellar and upper peristome insertions) ca. 25–45% of shell diameter. Peristome simple, unreflected, roundish: aperture height-width ratio (inside dimension, height measured to and perpendicular to a line between the columellar and upper peristome insertions) 0.8–1.0. Distance between columellar and upper peristome insertions is 50–75% of aperture width. Penultimate whorl projecting into body whorl; occupying 4–16% of aperture height measure. Umbilicus 21–34% of shell

diameter. Whorls of adults ca. 3.5–5.4. Coiling tightness (whorl number/ \ln diameter) 1.9–3.3. Embryonic whorls 1.4–1.7; diameter 1.0–1.6 mm. First-whorl diameter 0.8–1.2 mm. Embryonic sculpture obliquely crosshatched. Post-embryonic shell sculpture of transverse ribs, 7–26 ribs in the first one-tenth of the body whorl; rib height 0.5–1.0% of shell diameter; rib periostracum without ornamentation or locally extended into hairs. Peripheral, non-rib periostracum without ornamentation or locally extended into hairs. Spiral sculpture absent or restricted to a few spiral grooves below the periphery of the body whorl. Shell basic color yellow-brown to brown-red. Secondary coloration absent or consisting of whitish flammulations or blotches.

Penis length 0.4–0.9 shell diameter, thick, slightly bulbous apically. Penis without sheath or caecum. Penial sculpture consisting of various combinations of smooth (rarely pustulose), soft bulges, flaps, pilasters, and ridges. Epiphallus a bulbous sac arising subterminally from the apical penial bulb; epiphallar bulb lying alongside, and tightly adherent to, the apical penial bulb. Spermatophore less than three times as long as wide, tapered, spiraling slightly; spermatophore attaches to the mate's basal penis. Penial retractor muscle attached to the epiphallar bulb, below the bulb's apex. Vas deferens enters the epiphallus basally, near the epiphallus's juncture with the penis; vas deferens slender along its entire length. Atrium short to long. Spermathecal duct joining the oviduct near the oviduct's entry to the atrium, thus the vagina is short. Spermathecal duct slender; spermatheca unknown. Fertilization pouch-seminal receptacle complex extremely long and slender, generally free of the albumen gland.

Diagnosis: *Reticulapex* gen. nov. seems to be a monophyletic clade diagnosed by, and unique for, its obliquely cross-hatched embryonic sculpture; an extremely elongate fertilization pouch-seminal receptacle complex; nearly basal entry of the vas deferens into, and nearly apical origin of the penial-retractor muscle from, the epiphallus; and a spiral spermatophore that is transferred to the mate's basal penis.

Comments: *Reticulapex* gen. nov. and *Trachycystis* Pilsbry, 1893, seem to be the only genera of Charopidae known so far in Madagascar. We have collected extensively in Tsaratanana Reserve and found species very similar to "*Pilula*" *excavata* Fischer-Piette, Blanc & Salvat, 1975, and "*Pilula*" *madecassina* Fischer-Piette, Blanc & Salvat, 1975, of the same massif; they are not *Pilula* Martens, 1898, but seem to be Helicarionidae, tentatively *Microcystis* Beck, 1837 (Emberton, unpublished). Surprisingly, we did not find any Charopidae in Tsaratanana Reserve (Emberton, unpublished).

"*Pilula*" *harananae* Emberton, 1994; "*Pilula*" *talatai* Emberton, 1994; and "*Pilula*" *vatuvavyae* Emberton, 1994, are not *Pilula*, but *Reticulapex* gen. nov.

Trachycystis is currently assigned to Charopidae

(Vaught, 1989), not Punctidae as erroneously stated by Fischer-Piette et al. (1994). Only one of Fischer-Piette et al.'s (1994) "*Trachycystis*" seems validly placed: *Trachycystis waterloti* Fischer-Piette, Blanc, Blanc & Salvat, 1994. Their other species of "*Trachycystis*" are either *Reticulapex* gen. nov. (five species listed above) or, in all likelihood, Helicarionidae, tentatively either *Microcystis* or *Sitala* Adams, 1865 (Emberton, unpublished).

The spermatophore is known so far only in *R. compactus* sp. nov. and in the type species *R. villosus* sp. nov.

Reticulapex subangulatus Emberton & Pearce, sp. nov.

(Figures 1, 13, 18)

Charopidae sp. 1, Emberton et al., 1996:210. Emberton, 1997:1146, 1149. Emberton et al., 1999:table 2.

Holotype: USNM 860810 (ex MBI 383.02DH, Tol-11, ad).

Paratypes: MBI 380.14DP (4 ad, 6 juv), MBI 382.15DP (1 ad, 5 juv; AMS C.203454 [1 ad]; MNHN [1 ad]; ANSP 400836 [1 ad], MBI 382.15AP (2 ad [1 dissected], 1 juv), MBI 383.02DP (2 ad, 4 juv), MBI 384.14DP (2 ad, 3 juv), MBI 384.14AP (1 juv).

Type locality: Madagascar: Tulear Province: northwest of Fort Dauphin: west of village of Malio: southeast slope of Mount Vasiha, 700 m elevation: latitude 24°55'23"S, longitude 46°44'27"E: primary rainforest.

Description of holotype shell:

Shell Size and Shape. Diameter 7.8 mm; height 4.6 mm. Height-diameter ratio 0.6. Spire angle 130 degrees. Whorl periphery slightly angular. Whorl shoulder very flat. Aperture width (inside dimension, parallel to a line between the columellar and upper peristome insertions) 36% of shell diameter. Aperture height-width ratio (inside dimension, height measured to and perpendicular to a line between the columellar and upper peristome insertions) 1.0. Distance between columellar and upper peristome insertions is 61% of aperture width. Penultimate whorl projecting into body whorl; occupying 11% of aperture height measure. Umbilicus 26% of shell diameter. Whorls 4.1. Coiling tightness 2.0.

Embryonic Shell. Whorls 1.4; diameter 1.2 mm. First-whorl diameter 1.0 mm. Coiling tightness (embryonic whorl number divided by natural logarithm of embryonic shell diameter) 7.7. Embryonic sculpture crosshatched.

Shell Sculpture and Color. Neanic cross-hatch sculpture very faint. Transverse rib density 10 in first tenth of body whorl. Rib height 1.0% of shell diameter. Rib periostracum without ornamentation. Non-rib periostracum without ornamentation. Spiral sculpture absent or inconspicuous. Shell basic color yellow-brown. Secondary coloration absent.

Shell variation: Occasional shells have a slightly less angular periphery.

Shell comparisons: Most similar to *Reticulapex druggi* comb. nov., but more than 50% larger with fewer whorls.

Description of lower reproductive system (MBI 382.15AP: 1 adult): Penis 4.7 mm long (0.6 shell diameter), 1.0–1.4 mm wide, slightly bulbous apically. Penis without sheath or caecum. Penial sculpture consisting of a long apical flap (ca. 2.0 mm unfurled) and an elongate lateral bulge (ca. 1.7 mm long). Epiphallus a bulbous sac arising subterminally from the apical penial bulb; epiphallar bulb lying alongside, and tightly adherent to, the apical penial bulb. Penial retractor muscle attached to the epiphallar bulb, below the bulb's apex. Vas deferens enters the epiphallus basally, near the epiphallus's juncture with the penis; vas deferens slender along its entire length. Atrium short. Spermathecal duct joining the oviduct near the oviduct's entry to the atrium, thus the vagina is short. Spermathecal duct slender and long; spermatheca ovoid, lying alongside the proximal albumen gland. Fertilization pouch-seminal receptacle complex extremely long (ca. 2.5 mm) and slender, free of the albumen gland.

Distribution and conservation status: Mts. Ilapiry and Vasiha, 300 to 860 m elevation. Not known from any other localities (Emberton, unpublished). Thus, occurring as fragmented subpopulations within < 1000 km² of declining forest in the southern Anosy and Vohimena Chains, therefore, by IUCN (1996) criteria, an Endangered species.

Etymology: For the sub-angulate periphery.

Reticulapex lucidus Emberton & Pearce, sp. nov.

(Figures 2, 14, 19)

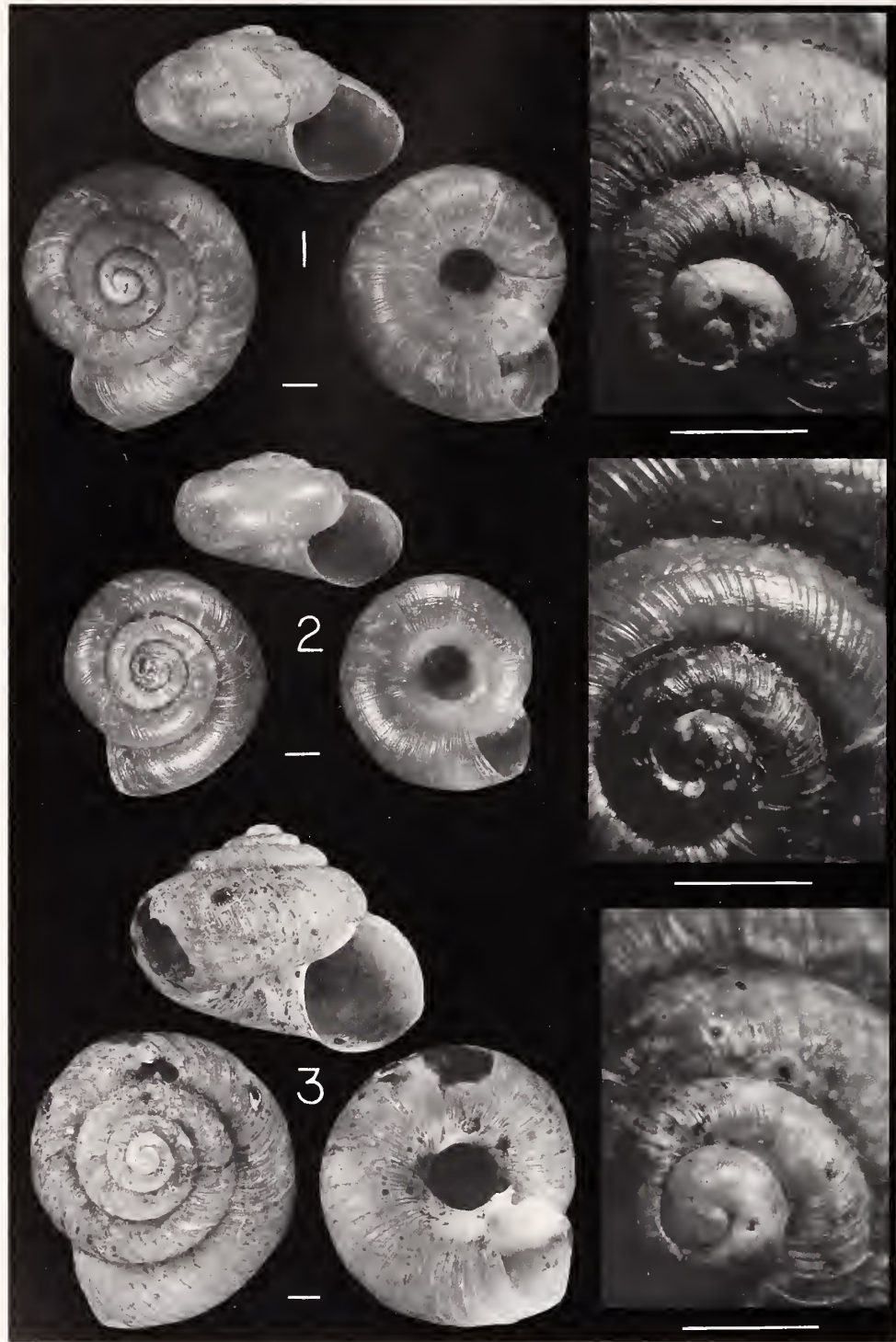
Charopidae n. gen. *ulrichi* Fischer-Piette et al., 1994, Emberton, 1996:736 (due to a printer's error replacing "n. sp. 13," rather than the correct "n. sp. 14," with "*ulrichi*").

Charopidae sp. 2, Emberton et al., 1996:210. Emberton, 1997:1146, 1149. Emberton et al., 1999:table 2.

Holotype: USNM 860811 (ex MBI 378.03DH, Tol-6, ad).

Paratypes: MBI 377.15DP (10 ad, 30 juv), MBI 377.15AP (13 juv), MBI 378.03DP (10 ad, 21 juv; AMS C.203455 [1 ad]; MNHN [1 ad]; ANSP 400837 [1 ad]), MBI 378.03AP (1 ad [dissected], 13 juv), MBI 379.22DP (4 ad, 9 juv), MBI 379.22AP (6 juv), MBI 380.15DP (6 ad, 10 juv), MBI 380.15AP (3 ad, 5 juv), MBI 381.15DP (8 ad, 17 juv), MBI 381.15AP (2 ad, 4 juv), MBI 382.16DP (2 juv), MBI 382.16AP (1 juv), MBI 388.09DP (1 juv), MBI 391.06AP (1 ad).

Type locality: Madagascar: Tulear Province: northwest



Figures 1-3

Figure 1. *Reticulapex subangulatus* Emberton & Pearce, sp. nov., holotype. Figure 2. *Reticulapex lucidus* Emberton & Pearce, sp. nov., holotype. Figure 3. *Reticulapex scaber* Emberton & Pearce, sp. nov., holotype. All scale bars 1 mm.

of Fort Dauphin: west of village of Mahialambo: ridge on east slope of Mt. Ilapiry, 500 m elevation, latitude 24°51'33"S, longitude 47°00'27"E: primary rainforest.

Description of holotype shell:

Shell Size and Shape. Diameter 6.6 mm; height 3.9 mm. Height-diameter ratio 0.6. Spire angle 140 degrees. Whorl periphery round. Whorl shoulder round. Aperture width (inside dimension, parallel to a line between the columellar and upper peristome insertions) 41% of shell diameter. Aperture height-width ratio (inside dimension, height measured to and perpendicular to a line between the columellar and upper peristome insertions) 0.9. Distance between columellar and upper peristome insertions is 63% of aperture width. Penultimate whorl projecting into body whorl; occupying 13% of aperture height measure. Umbilicus 25% of shell diameter. Whorls 4.3. Coiling tightness 2.3.

Embryonic Shell. Whorls 1.7; diameter 1.2 mm. First-whorl diameter 1.1 mm. Coiling tightness (embryonic whorl number divided by natural logarithm of embryonic shell diameter) 9.3. Embryonic sculpture crosshatched.

Shell Sculpture and Color. Neanic cross-hatch sculpture very faint. Transverse rib density 15 in first tenth of body whorl. Rib height 0.5% of shell diameter. Rib periostracum without ornamentation. Non-rib periostracum without ornamentation. Spiral sculpture conspicuous; 10 grooves below periphery of body whorl. Shell basic color brown-yellow. Secondary coloration absent.

Shell variation: Some shells have a noticeably higher spire than the holotype.

Shell comparisons: Much tighter coiling than *Reticulapex ulrichi* comb. nov.

Description of lower reproductive system (MBI 378.03AP: 1 adult): Penis 3.8 mm long (0.6 shell diameter), 0.8–1.1 mm wide, slightly bulbous apically. Penis without sheath or caecum. Penial sculpture consisting of a long apical flap (ca. 1.7 mm unfurled); an elongate lateral bulge (ca. 1.5 mm long); and a parallel, crestlike pilaster (ca. 2.0 mm long). Epiphallus a bulbous sac arising subterminally from the apical penial bulb; epiphallar bulb lying alongside, and tightly adherent to, the apical penial bulb. Penial retractor muscle attached to the epiphallar bulb, below the bulb's apex. Vas deferens enters the epiphallus basally, near the epiphallus's juncture with the penis; vas deferens slender along its entire length. Atrium long. Spermathecal duct joining the oviduct near the oviduct's entry to the atrium, thus the vagina is short. Spermathecal duct slender and long; spermatheca ovoid, lying alongside the proximal albumen gland. Fertilization pouch-seminal receptacle complex extremely long (ca. 2.2 mm) and slender, free of the albumen gland.

Distribution and conservation status: Mts. Ilapiry and Vasiha, 200 to 860 m elevation. Also reported from An-

dohahela (1200–1960 m) in the Anosy Chain, and from Mt. Teloboko (640 m, just below the summit), which is near Mt. Mahermana in the Vohimena Chain; but from nowhere else (Emberton, unpublished). Thus an Endangered species by IUCN (1996) criteria: restricted to < 2000 km² of forest that is continually declining in extent and quality, and occurring as isolated subpopulations.

Etymology: For the shell surface being relatively shiny (*L. lucid-*) for the genus.

Reticulapex scaber Emberton & Pearce, sp. nov.

(Figure 3)

Charopidae n. gen. n. sp. 12, Emberton, 1996:736.

Charopidae sp. 3, Emberton et al., 1996:210. Emberton 1997:1147, 1150. Emberton et al., 1999:table 2.

Holotype: USNM 860812 (ex MBI 376.04DH, Tol-4, ad).

Paratypes: MBI 374.16DP (2 juv), MBI 375.14DP (1 ad, 2 juv; AMS C.203456 [1 ad]), MBI 376.04DP (2 juv), MBI 376.04AP (1 juv).

Type locality: Madagascar: Tulear Province: northwest of Fort Dauphin: northeast of village of Esetra: valley on northwest slope of Mt. Mahermana, 100 m elevation: latitude 24°26'22"S, longitude 47°12'41"E: primary rainforest.

Description of holotype shell:

Shell Size and Shape. Diameter 8.6 mm; height 6.6 mm. Height-diameter ratio 0.8. Spire angle 110 degrees. Whorl periphery round. Whorl shoulder flat. Aperture width (inside dimension, parallel to a line between the columellar and upper peristome insertions) 41% of shell diameter. Aperture height-width ratio (inside dimension, height measured to and perpendicular to a line between the columellar and upper peristome insertions) 1.0. Distance between columellar and upper peristome insertions is 49% of aperture width. Penultimate whorl projecting into body whorl; occupying 9% of aperture height measure. Umbilicus 23% of shell diameter. Whorls 4.9. Coiling tightness 2.3.

Embryonic Shell. Whorls 1.6; diameter 1.4 mm. First-whorl diameter 0.9 mm. Coiling tightness (embryonic whorl number divided by natural logarithm of embryonic shell diameter) 4.8. Embryonic sculpture crosshatched.

Shell Sculpture and Color. Neanic cross-hatch sculpture strong. Transverse rib density 7 in first tenth of body whorl. Rib height 1.6% of shell diameter. Rib periostracum without ornamentation. Non-rib periostracum without ornamentation. Spiral sculpture absent or inconspicuous. Shell basic color brown-yellow. Secondary coloration absent.

Shell variation: No conspicuous variation in size or shape.

Shell comparisons: Most similar to *Reticulapex vineti* comb. nov., but larger for the same number of whorls and lacking a caniculate suture and flamulate coloration.

Distribution and conservation status: Mt. Mahermana, 100 to 300 m elevation. Also reported from the nearby Mts. Teloboko (640 m) and Esetra (mid-elevational slope), and from the central-Vohimana-chain Mt. Varabe (200 m), but nowhere else (Emberton, unpublished). Thus this species appears to be restricted to the northern Vohimana Mountain Chain. Its forest habitat covers < 400 km² that is diminishing rapidly in area and quality, and it is fragmented into isolated subpopulations with reduced probability of recolonization. By IUCN (1996) criteria, *Reticulapex* gen. nov. *scaber* sp. nov. is Endangered.

Etymology: For the rough (*L. scaber*) surface sculpture.

Reticulapex compactus Emberton & Pearce, sp. nov.

(Figures 4, 15, 20)

Charopidae sp. 4, Emberton et al., 1996:210. Emberton, 1997:1146, 1150. Emberton et al., 1999:table 2.

Holotype: USNM 860813 (ex MBI 373.08DH, Tol-1, ad).

Paratypes: MBI 373.08DP (1 ad, 1 juv), MBI 373.08AP (2 ad [1 dissected], 3 juv), MBI 374.17DP (2 ad, 7 juv; AMS C.203457 [1 ad]; MNHN [1 ad]; ANSP 400838 [1 ad]), MBI 375.15DP (5 ad, 3 juv), MBI 375.15AP (1 ad, 2 juv).

Type locality: Madagascar: Tulear Province: northwest of Fort Dauphin: northeast of village of Esetra: summit of Mt. Mahermana, 340 m elevation: latitude 24°26'12"S, longitude 47°13'13"E: primary rainforest.

Description of holotype shell:

Shell Size and Shape. Diameter 3.3 mm; height 2.6 mm. Height-diameter ratio 0.8. Spire angle 100 degrees. Whorl periphery round. Whorl shoulder round. Aperture width (inside dimension, parallel to a line between the columellar and upper peristome insertions) 42% of shell diameter. Aperture height-width ratio (inside dimension, height measured to and perpendicular to a line between the columellar and upper peristome insertions) 0.8. Distance between columellar and upper peristome insertions is 75% of aperture width. Penultimate whorl projecting into body whorl; occupying 10% of aperture height measure. Umbilicus 23% of shell diameter. Whorls 3.9. Coiling tightness 3.3.

Embryonic Shell. Whorls 1.5; diameter 1.0 mm. First-whorl diameter 0.8 mm. Coiling tightness (embryonic whorl number divided by natural logarithm of embryonic shell diameter) 15.7. Embryonic sculpture crosshatched.

Shell Sculpture and Color. Neanic cross-hatch sculpture very faint. Transverse rib density 9 in first tenth of

body whorl. Rib height 0.6% of shell diameter. Rib periostracum without ornamentation. Non-rib periostracum without ornamentation. Spiral sculpture absent or inconspicuous. Shell basic color brown. Secondary coloration absent.

Shell variation: No conspicuous variation in size or shape.

Shell comparisons: Most similar to *Reticulapex kermadeci* comb. nov., but twice as large for the same number of whorls and with a proportionally smaller aperture.

Description of lower reproductive system (MBI 373.08AP: 1 adult):

Penis 2.0 mm long (0.6 shell diameter), 0.4–0.6 mm wide, slightly bulbous apically. Penis without sheath or caecum. Penial sculpture consisting of a thin apical pilaster (ca. 0.7 mm long), below which is an ovoid lateral bulge (ca. 0.7 mm long). Epiphallus a bulbous sac arising subterminally from the apical penial bulb; epiphallar bulb lying alongside, and tightly adherent to, the apical penial bulb. Spermatophore consisting of an egg-shaped body (ca. 0.6 mm long) with a stalklike process (ca. 0.6 mm long) that spirals slightly; spermatophore found attached within the basal penial tube. Penial retractor muscle attached to the epiphallar bulb, below the bulb's apex. Vas deferens enters the epiphallus basally, near the epiphallus's juncture with the penis; vas deferens slender along its entire length. Atrium long. Spermathecal duct joining the oviduct near the oviduct's entry to the atrium, thus the vagina is short. Spermathecal duct slender and long; spermatheca ovoid, lying alongside the proximal albumen gland. Fertilization pouch-seminal receptacle complex unknown.

Distribution and conservation status: Mt. Mahermana, 200 to 340 m elevation. Also reported from a nearby patch of coastal forest at about 15 m elevation. This is a Critically Endangered species, by criteria of the IUCN (1996), because it is highly fragmented between two patches within < 100 km² of forest habitat that is continually declining in area and quality.

Etymology: For the compact shape.

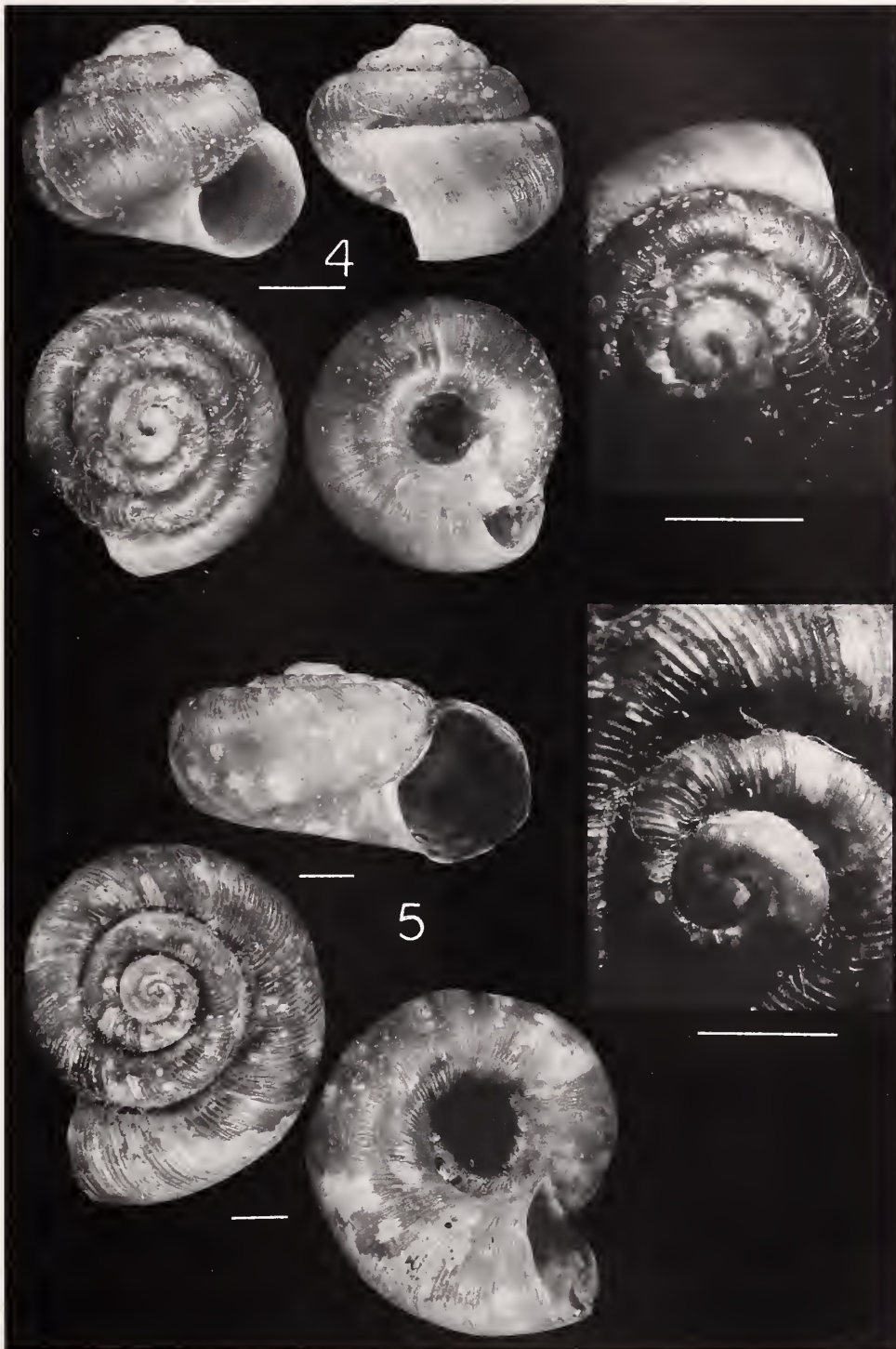
Reticulapex flammulatus Emberton & Pearce, sp. nov.

(Figure 5)

Charopidae sp. 5, Emberton et al., 1996:210. Emberton, 1997:1146, 1150. Emberton et al., 1999:table 2.

Holotype: USNM 860814 (ex MBI 377.03DH, Tol-5, ad).

Paratypes: MBI 373.17DP (1 juv), MBI 374.18DP (1 juv), MBI 375.16DP (3 juv), MBI 377.03DP (1 juv), MBI 377.03AP (4 juv), MBI 378.15DP (1 ad, 1 juv; AMS C.203458 [1 ad]; MNHN [1 ad]), MBI 379.23DP (1 ad).



Figures 4 and 5

Figure 4. *Reticulapex compactus* Emberton & Pearce, sp. nov., holotype. Figure 5. *Reticulapex flammulatus* Emberton & Pearce, sp. nov., holotype. All scale bars 1 mm.

Type locality: Madagascar: Tulear Province: northwest of Fort Dauphin: west of village of Mahialambo: summit of Mt. Ilapiry, 540 m elevation: latitude 24°51'40"S, longitude 47°00'20"E: primary rainforest.

Description of holotype shell:

Shell Size and Shape. Diameter 6.5 mm; height 3.6 mm. Height-diameter ratio 0.6. Spire angle 150 degrees. Whorl periphery round. Whorl shoulder round. Aperture width (inside dimension, parallel to a line between the columellar and upper peristome insertions) 40% of shell diameter. Aperture height-width ratio (inside dimension, height measured to and perpendicular to a line between the columellar and upper peristome insertions) 0.9. Distance between columellar and upper peristome insertions is 55% of aperture width. Penultimate whorl projecting into body whorl; occupying 10% of aperture height measure. Umbilicus 34% of shell diameter. Whorls 3.8. Coiling tightness 2.0.

Embryonic Shell. Whorls 1.6; diameter 1.6 mm. First-whorl diameter 1.1 mm. Coiling tightness (embryonic whorl number divided by natural logarithm of embryonic shell diameter) 3.4. Embryonic sculpture crosshatched.

Shell Sculpture and Color. Neanic cross-hatch sculpture faint. Transverse rib density 14 in first tenth of body whorl. Rib height 0.6% of shell diameter. Rib periostracum without ornamentation. Non-rib periostracum without ornamentation. Spiral sculpture absent or inconspicuous. Shell basic color brown-red. Secondary coloration white blotches.

Shell variation: No conspicuous variation in size or shape.

Shell comparisons: Larger, flatter, and more loosely coiled than *Reticulapex intridi* comb. nov. Fewer whorls (but same size) and much stronger ribbed sculpture than *Reticulapex vatuvayae* comb. nov.

Distribution and conservation status: Mts. Mahermana and Ilapiry, 200 to 540 m elevation. Not known from any other localities, not even from several peaks adjacent to Mt. Mahermana (Emberton, unpublished). Clearly an Endangered species (IUCN [1996] criteria), restricted to fragmented subpopulations within the Vohimena Chain, whose forests extend only about 500 km² and are continually declining.

Etymology: For the flame-colored (*L. flamma*) markings on the shell.

Reticulapex fischerpiettei Emberton & Pearce, sp. nov.

(Figure 6)

Charopidae n. gen. n. sp. 10, Emberton, 1996:736.

Charopidae sp. 6, Emberton et al., 1996:210. Emberton, 1997:1146, 1150. Emberton et al., 1999:table 2.

Holotype: USNM 860815 (ex MBI 379.03DH, Tol-7, ad).

Paratypes: MBI 379.03DP (2 ad, 2 juv; AMS C.203459 [1 ad]; MNHN [1 ad]; ANSP 400839 [1 ad]), MBI 379.03AP (2 juv), MBI 380.16DP (1 ad, 4 juv), MBI 381.16DP (3 ad, 7 juv), MBI 381.16AP (3 juv).

Type locality: Madagascar: Tulear Province: northwest of Fort Dauphin: west of village of Mahialambo: ridge, valley, and slope on southsoutheast slope of Mt. Ilapiry, 400m elevation: latitude 24°51'27"S, longitude 47°00'38"E: primary rainforest.

Description of holotype shell:

Shell Size and Shape. Diameter 3.9 mm; height 2.8 mm. Height-diameter ratio 0.7. Spire angle 100 degrees. Whorl periphery slightly angular. Whorl shoulder very flat. Aperture width (inside dimension, parallel to a line between the columellar and upper peristome insertions) 38% of shell diameter. Aperture height-width ratio (inside dimension, height measured to and perpendicular to a line between the columellar and upper peristome insertions) 0.9. Distance between columellar and upper peristome insertions is 54% of aperture width. Penultimate whorl projecting into body whorl; occupying 4% of aperture height measure. Umbilicus 23% of shell diameter. Whorls 3.8. Coiling tightness 2.8.

Embryonic Shell. Whorls 1.5; diameter 1.2 mm. First-whorl diameter 0.9 mm. Coiling tightness (embryonic whorl number divided by natural logarithm of embryonic shell diameter) 8.2. Embryonic sculpture crosshatched.

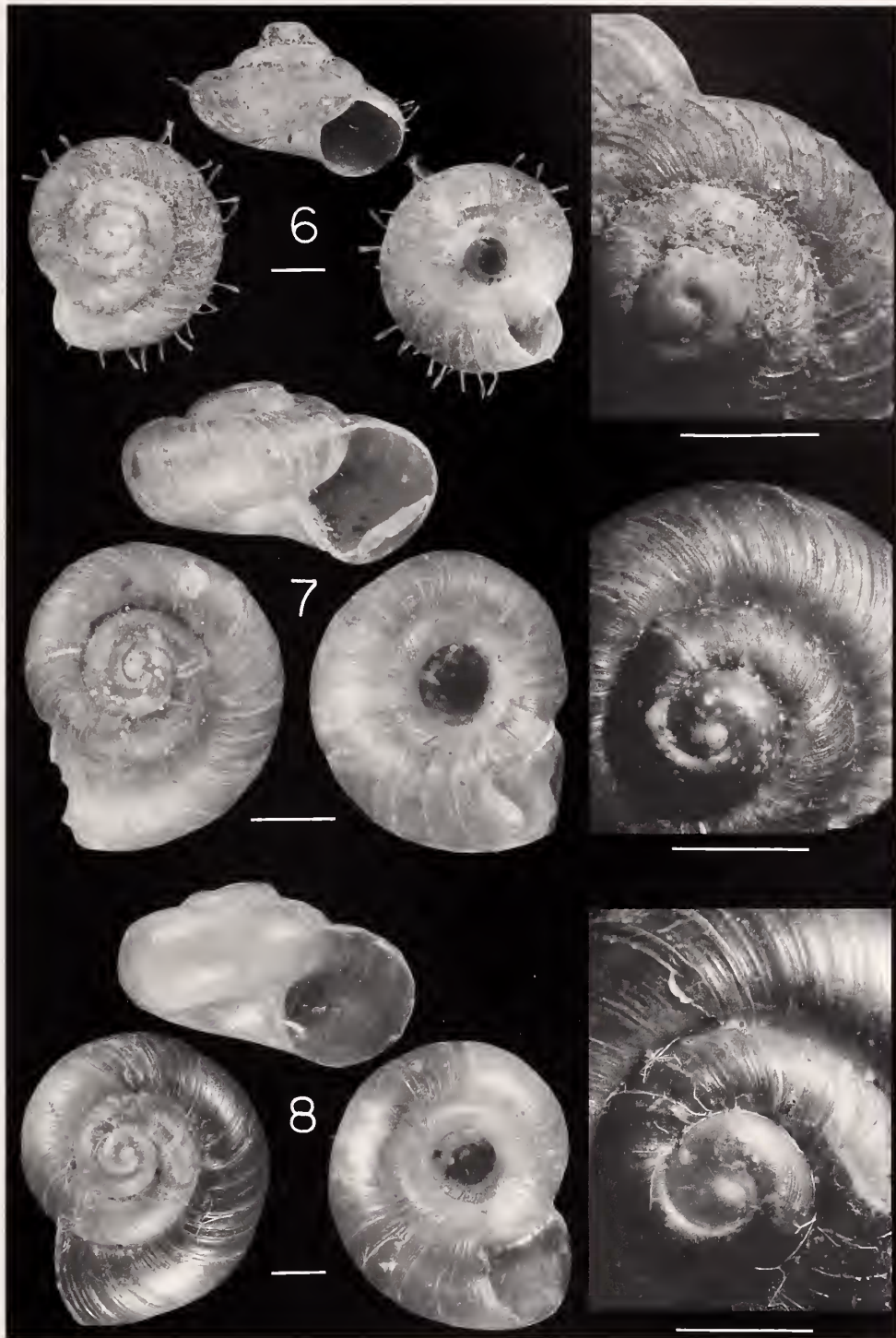
Shell Sculpture and Color. Neanic cross-hatch sculpture moderate. Transverse rib density 8 in first tenth of body whorl. Rib height 1.0% of shell diameter. Rib periostracum locally extended into hairs; hair length 12.8% of shell diameter. Non-rib periostracum without ornamentation. Spiral sculpture absent or inconspicuous. Shell basic color brown-red. Secondary coloration absent.

Shell variation: No conspicuous variation in size or shape.

Shell comparisons: Unique within the genus for its lenticular shape and long peripheral hairs.

Distribution and conservation status: Mt. Ilapiry, 200 to 400 m elevation. Also reported (Emberton, unpublished) from the nearby Mt. St. Jacques (520 m) and, in the Anosy Chain, from Andohahela (1400–1600 m); but nowhere else. Thus fragmented within the southern Vohimena and Anosy forests, whose extent is < 1000 km² and is continually declining; therefore, by IUCN (1996) standards, an Endangered species.

Etymology: For the late E. Fischer-Piette, longtime systematist of Madagascar's land snails.



Figures 6–8

Figure 6. *Reticulapex fischerpiettei* Emberton & Pearce, sp. nov., holotype. Figure 7. *Reticulapex apexfortis* Emberton & Pearce, sp. nov., holotype. Figure 8. *Reticulapex ulrichi* (Fischer-Piette, Blanc, Blanc & Salvat, 1994) comb. nov., representative from Mt. Vasiha at 100 m elevation. All scale bars 1 mm.

Reticulapex apexfortis Emberton & Pearce, sp.
nov.

(Figure 7)

Charopidae sp. 7, Emberton et al., 1996:210. Emberton, 1997:1147. Emberton et al., 1999:table 2.

Holotype: USNM 860816 (ex MBI 384.03DH, Tol-12, ad).

Paratypes: MBI 384.03DP (1 juv), MBI 384.03AP (2 juv).

Type locality: Madagascar: Tulear Province: northwest of Fort Dauphin: west of village of Malio: east slope of Mt. Vasiha, 500 m elevation: latitude 24°55'19"S, longitude 46°44'45"E: primary rainforest.

Description of holotype shell:

Shell Size and Shape. Diameter 3.6 mm; height 2.2 mm. Height-diameter ratio 0.6. Spire angle 140 degrees. Whorl periphery round. Whorl shoulder round. Aperture width (inside dimension, parallel to a line between the columellar and upper peristome insertions) 43% of shell diameter. Aperture height-width ratio (inside dimension, height measured to and perpendicular to a line between the columellar and upper peristome insertions) 0.9. Distance between columellar and upper peristome insertions is 49% of aperture width. Penultimate whorl projecting into body whorl; occupying 16% of aperture height measure. Umbilicus 26% of shell diameter. Whorls 3.2. Coiling tightness 2.5.

Embryonic Shell. Whorls 1.5; diameter 1.3 mm. First-whorl diameter 0.8 mm. Coiling tightness (embryonic whorl number divided by natural logarithm of embryonic shell diameter) 6.5. Embryonic sculpture crosshatched.

Shell Sculpture and Color. Neanic cross-hatch sculpture faint. Transverse rib density 9 in first tenth of body whorl. Rib height 0.8% of shell diameter. Rib periostracum without ornamentation. Non-rib periostracum without ornamentation. Spiral sculpture absent or inconspicuous. Shell basic color brown. Secondary coloration absent.

Shell comparisons: Similar to *Reticulapex choutardi* comb. nov., but without its complex embryonic sculpture, without its spiral sculpture, and with a higher spire (height/diameter 0.8 as opposed to 0.6).

Distribution and conservation status: Known only from Mt. Vasiha at 500 m elevation. No records elsewhere (Emberton, unpublished). By IUCN (1996) criteria (single locality, < 100 km² extent, continuing decline in area and quality of habitat), *Reticulapex* gen. nov. *apexfortis* sp. nov. is Critically Endangered.

Etymology: For the strong (*L. fortis*) sculpturing on its embryonic whorls, or tip (*L. apex*).

Reticulapex ulrichi

(Fischer-Piette, Blanc, Blanc & Salvat, 1994)
comb. nov.

(Figures 8, 16, 21)

Trachycystis ulrichi n. sp., Fischer-Piette et al., 1994:175–177, fig. 71.

Charopidae n. gen. n. sp. 3, Emberton, 1996:736.

Charopidae n. gen. n. sp. 14 (not "n. gen. *ulrichi*," which was a printer's error), Emberton, 1996:736.

Charopidae sp. 8, Emberton et al., 1996:210. Emberton, 1997:1147. Emberton et al., 1999:table 2.

Representative: MBI 388.01DR, Tol-16 (ad).

Other specimens: MBI 388.01A (1 ad [dissected]).

Description of representative:

Shell Size and Shape. Diameter 5.4 mm; height 3.3 mm. Height-diameter ratio 0.6. Spire angle 140 degrees. Whorl periphery round. Whorl shoulder round. Aperture width (inside dimension, parallel to a line between the columellar and upper peristome insertions) 46% of shell diameter. Aperture height-width ratio (inside dimension, height measured to and perpendicular to a line between the columellar and upper peristome insertions) 0.9. Distance between columellar and upper peristome insertions is 50% of aperture width. Penultimate whorl projecting into body whorl; occupying 12% of aperture height measure. Umbilicus 25% of shell diameter. Whorls 3.3. Coiling tightness 2.0.

Embryonic Shell. Whorls 1.5; diameter 1.5 mm. First-whorl diameter 1.1 mm. Coiling tightness (embryonic whorl number divided by natural logarithm of embryonic shell diameter) 3.7. Embryonic sculpture crosshatched.

Shell Sculpture and Color. Neanic cross-hatch sculpture absent (undetected). Transverse rib density 8 in first tenth of body whorl. Rib height 0.2% of shell diameter. Rib periostracum without ornamentation. Non-rib periostracum without ornamentation. Non-rib periostracum without ornamentation. Spiral sculpture absent or inconspicuous. Shell basic color brown-yellow. Secondary coloration absent.

Description of lower reproductive system (MBI

388.01A: 1 adult): Penis 5.0 mm long (0.9 shell diameter), 0.8–1.2 mm wide, slightly bulbous apically. Penis without sheath or caecum. Penial sculpture consisting of two parallel apical pilasters (ca. 2.5 mm long), below one of which is an ovoid lateral bulge (ca. 1.5 mm long). Epiphallus a bulbous sac arising subterminally from the apical penial bulb; epiphallar bulb lying alongside, and tightly adherent to, the apical penial bulb. Penial retractor muscle attached to the epiphallar bulb, below the bulb's apex. Vas deferens enters the epiphallus basally, near the epiphallus's juncture with the penis; vas deferens slender along its entire length. Atrium short. Spermathecal duct joining the oviduct near the oviduct's entry to the atrium,

thus the vagina is short. Spermathecal duct slender and long; spermatheca ovoid, lying alongside the proximal albumen gland. Fertilization pouch-seminal receptacle complex extremely long (ca. 5 mm) and slender.

Distribution and conservation status: Mt. Vasiha at 100 m elevation. Described (Fischer-Piette et al., 1994) from elsewhere in the Anosy Chain, 1000–1950 m. Emberton (unpublished) gives records from Andohahela (450–1900 m), Col Beampingaratra (380–1280 m), Mt. Ramabeafo (410–700 m), and other localities in the southern Anosy Chain and in the ridge connecting it to the southern Vohimena Chain; as well as in the northern, but not the southern, Vohimena Chain: Mt. Mahermana (300 m) and Mt. Varabe (200 m). With a range restricted to the Anosy and northern Vohimena Chains, this species is Endangered, under IUCN criteria (IUCN, 1996: occurrence < 5000 km², severely fragmented, habitat extent and quality in continuing decline).

Reticulapex villosus Emberton & Pearce, sp. nov.

(Figures 9, 10, 11, 12, 17, 22, 23)

Charopidae n. gen. n. sp. 11. Emberton, 1996:736.

Charopidae sp. 9. Emberton et al., 1996:210. Emberton, 1997:1147, 1150. Emberton et al., 1999:table 2.

Holotype: USNM 860817 (ex MBI 389.01DH, Tol-3-4, ad).

Paratypes: MBI 373.26AP (1 ad), MBI 374.25AP (2 juv), MBI 375.22AP (3 ad [1 dissected], 2 juv), MBI 389.01AP (2 ad [1 dissected]), MBI 390.02DP (0; AMS C.203460 [1 ad]).

Type locality: Madagascar: Tulear Province: northwest of Fort Dauphin: northeast of village of Esetra: west slope of Mt. Mahermana, 100–200 m elevation, latitude 24°26'15–22"S, longitude 47°13'04–12".41E: primary rainforest.

Description of holotype shell:

Shell Size and Shape. Diameter 18.1 mm; height 10.2 mm. Height-diameter ratio 0.6. Spire angle 140 degrees. Whorl periphery round. Whorl shoulder flat. Aperture width (inside dimension, parallel to a line between the columellar and upper peristome insertions) 38% of shell diameter. Aperture height-width ratio (inside dimension, height measured to and perpendicular to a line between the columellar and upper peristome insertions) 1.0. Distance between columellar and upper peristome insertions is 64% of aperture width. Penultimate whorl projecting into body whorl; occupying 13% of aperture height measure. Umbilicus 21% of shell diameter. Whorls 5.4. Coiling tightness 1.9.

Embryonic Shell. Whorls 1.7; diameter 1.6 mm. First-whorl diameter 1.2 mm. Coiling tightness (embryonic whorl number divided by natural logarithm of embryonic shell diameter) 3.6. Embryonic sculpture crosshatched.

Shell Sculpture and Color. Neanic cross-hatch sculpture absent (undetected). Transverse rib density 26 in first tenth of body whorl. Rib height 0.1% of shell diameter. Rib periostracum without ornamentation. Non-rib periostracum with bristles; 18 bristles in each inter-rib space between sutures at end of penultimate whorl; bristle length 1.3% of shell diameter. Spiral sculpture absent or inconspicuous. Shell basic color brown-red. Secondary coloration absent.

Shell variation: No conspicuous variation in size or shape.

Shell comparisons: Unique within the genus for its huge size and dense hairs.

Description of lower reproductive system (MBI 375.22AP: 1 adult; MBI 389.01AP: 1 adult): Penis 7.8 mm long (0.4 shell diameter), 1.4–2.5 mm wide, slightly bulbous apically. Penis without sheath or caecum. Penial sculpture consisting of an apical, ovoid, pustulose (glandular?) bulb (ca. 1.7 mm long); a thick, V-shaped pilaster in the upper half of the penis (length ca. 3.9 mm); a field of basal ridges that are low, parallel, and even (ca. 14 in number); and an indistinct basal pilaster (ca. 4.7 mm long). Epiphallus a bulbous sac arising subterminally from the apical penial bulb; epiphallar bulb lying alongside, and tightly adherent to, the apical penial bulb. Spermatophore thick-bodied, tapered apically, spiraling slightly (length ca. 3.4 mm); spermatophore found attached within the basal penial tube. Penial retractor muscle attached to the epiphallar bulb, below the bulb's apex. Vas deferens enters the epiphallus basally, near the epiphallus's juncture with the penis; vas deferens slender along its entire length. Atrium short. Spermathecal duct joining the oviduct near the oviduct's entry to the atrium, thus the vagina is short. Spermathecal duct slender; spermatheca unknown. Fertilization pouch-seminal receptacle complex extremely long (total length unknown) and slender, free of the albumen gland.

Distribution and conservation status: Mt. Mahermana, 200 to 340 m elevation. Also found on Mt. Varabe at 410 m, but nowhere else (Emberton, unpublished). Apparently restricted to the northern Vohimena Mountain Chain, fragmented into subpopulations within dwindling forest < 500 km² in extent. Therefore, by IUCN (1996) criteria, an Endangered species.

Etymology: For the hairy (*L. villos-*) shell surface.

CHAROPID CONSERVATION STATUSES

Analyses of individual species are given above in the species descriptions. To summarize, all nine of the charopid species are proposed as either Endangered or Critically Endangered. Two species should be listed as **Critically Endangered**: *R. apexfortis* sp. nov. and *Reticulapex compactus* sp. nov. The seven species that should be list-



Figures 9-11

Reticulapex villosus Emberton & Pearce, sp. nov. Figure 9. Holotype. Figure 10. Paratype, MBI 390.02DP. Figure 11. Other paratype, MBI 375.22AP. All scale bars 1 mm.

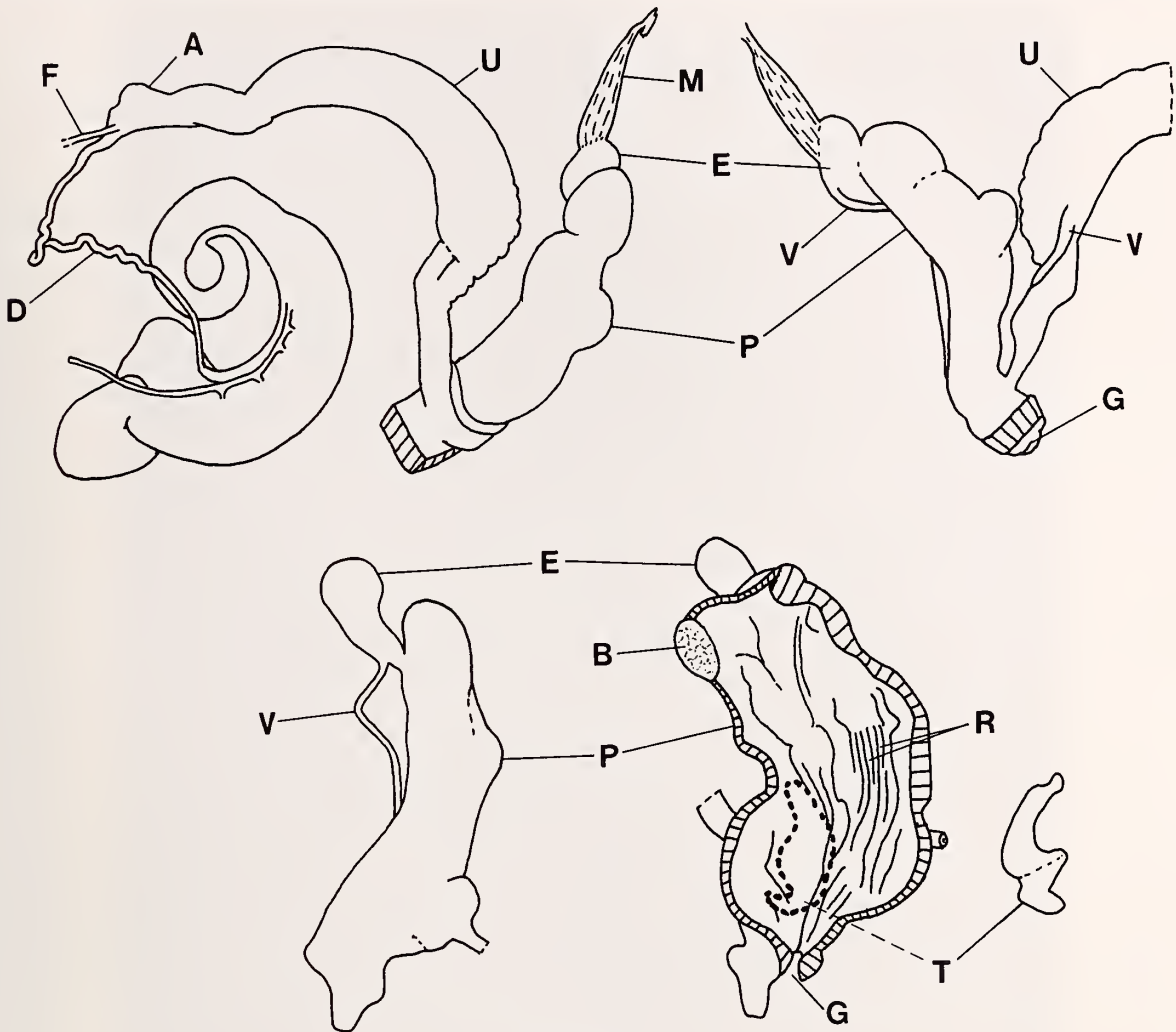


Figure 12

Some anatomical characters used in descriptions, as shown on *Reticulapex villosus* Emberton & Pearce, sp. nov. Abbreviations: A—albumen gland, B—pustulate bulb (penial sculpture), D—hermaphroditic duct, E—epiphallus, F—fertilization pouch—seminal receptacle complex (broken short in this specimen), G—genital pore, M—penial retractor muscle, P—penis, R—parallel ridges (penial sculpture), T—spermatophore (with deposition site), U—prostate-uterus, V—vas deferens.

ed as **Endangered** are: *R. fischerpiettei* sp. nov., *R. flammulatus* sp. nov., *R. lucidus* sp. nov., *R. scaber* sp. nov., *R. subangulatus* sp. nov., *R. ulrichi* (Fischer-Piette, Blanc, Blanc & Salvat, 1994) comb. nov., and *R. villosus* sp. nov.

DISCUSSION

These descriptions of nine charopids support our prior distributional and ecological analyses of Mahermana-Ilapiry-Vasiha land snails (Emberton et al., 1996, 1999; Emberton, 1997). Two previous papers (Emberton & Pearce, 1999, 2000) dealt with the caenogastropods and

the small, high-spired pulmonates. A fourth and final paper in this series is in press describing the Mahermana-Ilapiry-Vasiha helicarionids.

The Madagascan charopid radiation—contrary to an early prediction (Emberton, 1994a)—seems to be concentrated in the southeastern rainforests, with diversity dropping off steeply toward the north and with a total of 24 known species (Emberton, unpublished). Further exploration, particularly in the southeast, should yield many more species. Such exploration must be prompt, as much of the most diverse rainforest of the region will be soon be eradicated (Emberton, 1997; Emberton et al., 1999).



Figures 13–16

Charopid reproductive systems. Figure 13. *Reticulapex subangulatus* Emberton & Pearce, sp. nov. Figure 14. *Reticulapex lucidus* Emberton & Pearce, sp. nov. Figure 15. *Reticulapex compactus* Emberton & Pearce, sp. nov. Figure 16. *Reticulapex ulrichi* (Fischer-Piette, Blanc, Blanc & Salvat, 1994) comb. nov. All scale bars 1 mm.



Figures 17–23

Charopid reproductive systems, penes, and spermatophores. Figure 17. *Reticulapex villosus* Emberton & Pearce, sp. nov., MBI 375.22AP (right and left) and MBI 389.01AP (middle). Figure 18. *Reticulapex subangulatus* Emberton & Pearce, sp. nov. Figure 19. *Reticulapex lucidus* Emberton & Pearce, sp. nov. Figure 20. *Reticulapex compactus* Emberton & Pearce, sp. nov. Figure 21. *Reticulapex ulrichi* (Fischer-Piette, Blanc, Blanc & Salvat, 1994) comb. nov. Figures 22, 23, *Reticulapex villosus* Emberton & Pearce, sp. nov., MBI 375.22AP (Figure 22) and MBI 389.01AP (Figure 23). All scale bars 1 mm.

It seems very likely that that all but one (*Trachycystis waterloti*) of Madagascar's charopids belong to the endemic genus *Reticulapex* gen. nov. Fischer-Piette et al.'s (1994) "*Pilula*" seems to be helicarionid and should probably be transferred to *Microcystis* (this paper; Emberton, unpublished). *Reticulapex* gen. nov. seems to be a monophyletic clade defined by cross-hatched embryonic sculpture, a long FPSC, a distinctive epiphallus, and a spiral spermatophore that is transferred to the mate's basal penis.

Spermatophore placement on the mate's penis is known to occur only by external sperm exchange. This is a derived condition in which two mating snails evert and entwine, rather than insert, penes. External sperm exchange is apparently unique to stylommatophorans, within which it evolved independently in the Limacidae, Discidae, Succineidae, and Polygyridae (review in Emberton, 1994b).

Thus *Reticulapex* gen. nov. represents the fifth known independent evolution of external sperm exchange within the Stylommatophora. It is clear that external sperm exchange is not a general phenomenon within the Charopidae. Dissected charopids from Australia (Stanisic, 1990, 1993) and New Caledonia (Mordan & Tillier, 1986) have spermatophores within the female tract, implying internal sperm exchange.

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